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RESEARCH ARTICLE

Task-specific sensory coding strategies are matched to detection and discrimination performance

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ABSTRACT

The acquisition of sensory information is limited by the neural encoding method used, constraining perceptual abilities. The most relevant aspects of stimuli may change as behavioral context changes, making efficient encoding of information more challenging. Sensory systems must balance rapid detection of a stimulus with perception of fine details that enable discrimination between similar stimuli. Here, we show that in a species of weakly electric fish, *Apteronotus leptorhynchus*, two coding strategies are employed for these separate behavioral tasks. Using communication signals, we demonstrate a strong correlation between neural coding strategies and behavioral performance on a discrimination task. Extracellular recordings of pyramidal cells within the electrosensory lateral line lobe of alert fish show two distinct response patterns, either burst discharges with little variation between different signals of the same category, or a graded, heterogeneous response that contains sufficient information to discriminate between signals with slight variations. When faced with a discrimination-based task, the behavioral performance of the fish closely matches predictions based on coding strategy. Comparisons of these results with neural and behavioral responses observed in other model systems suggest that our study highlights a general principle in the way sensory systems utilize different neural codes.

KEY WORDS: Neural coding, Communication signals, Detection, Discrimination, Information theory, Weakly electric fish

INTRODUCTION

Behavioral context can dramatically affect the perception of sensory signals and the most relevant aspects of the signal can vary with these changes in context. Sometimes an organism merely needs to detect a specific signal within a continuous and noisy sensory stream. Alternatively, the organism might need to finely evaluate the properties of the signals in order to discriminate meaningful variations (Bradbury and Vehrencamp, 2011; Kröger et al., 2011; Mitchell et al., 2006; Oglesbee and Kewley-Port, 2009; Richards, 1981). Our goal in this study is to demonstrate that these two different sensory needs – detection versus discrimination – are met with different sensory coding schemes specialized for different contexts.

Neuroscience research has long been concerned with deciphering the relationship between the pattern of activity of sensory neurons and perception. The challenges faced when studying this question can be divided into three: understanding how relevant sensory information is represented in the neural code; probing sensory abilities through behavior; and correlating the two into a cohesive understanding of 'perception'. The relationship between the sensory codes and sensory abilities of organisms has been explored in many systems (e.g. Arabzadeh et al., 2003; Freedman et al., 2001; Tremblay et al., 1996; von Heimendahl et al., 2007). In the visual and vibrissae systems, neural codes change as adaptation to a stimulus sets in. After adaptation, the initial low-threshold detectability of a novel stimulus is traded for increased discriminability between similar stimuli (Fairhall et al., 2001; Moore, 2004), a change reflected in the behavioral performance of the animal (Ollerenshaw et al., 2014).

The two neural coding schemes observed in this system have repeatedly been linked with detection versus discrimination tasks in various other systems. The first coding strategy relies on synchronous high-frequency firing – typically bursting – over a population, for detection of important stimulus features (Krahe and Gabbiani, 2004; Marsat and Pollack, 2012). The second relies on graded responses with heterogeneous firing across the population to support the evaluation and discrimination of fine details of the stimulus (Marsat et al., 2012; Panzeri et al., 2015; Tripathy et al., 2013). The relationship between these two strategies and stimulus encoding is firmly established, but we have yet to demonstrate that they indeed are systematically mediating different behavioral tasks. Here, we use the weakly electric fish communication system to demonstrate a close association between the stimulus-encoding method and the associated behavior. We propose a general principle linking these sensory codes to two different perceptual tasks: detection versus discrimination.

Weakly electric fish communication signals, or chirps, are transient modulations of their ongoing oscillating electric field or electric organ discharge (EOD). Two fish interacting will perceive each other's field as quasi-sinusoidal modulations of their own EOD (beats) and chirps as transient disruptions of this regular background. In typical male–female courtship interactions, signals will consist of high-frequency beats (HFBs) because of the sexual dimorphism of EOD frequency. Type 1 (big) chirps are produced most often in this context (Hagedorn and Heiligenberg, 1985; Hupé and Lewis, 2008). Low-frequency beats (LFBs) are more typical of same-sex encounters such as male–male aggressive interactions. LFBs elicit the production of frequent type 2 (small) chirps (Hupé and Lewis, 2008). Neurophysiological recordings of the primary electrosensory area in the brain, the electrosensory lateral line lobe (ELL), show that small chirps on LFBs are encoded by synchronized bursting among the population of pyramidal cells (Marsat et al., 2009), consistent with a feature-detection code. Courtship signals, big chirps on HFBs, are encoded via graded, heterogeneous firing (Marsat and Maler, 2010). This latter response type, but not the former, can support the efficient discrimination of small variations in chirp properties, possibly to evaluate the quality of the courtship signal.

LFBs and small chirps are typically associated with agonistic encounters, whereas HFBs and big chirps have been suggested as

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typical courtship signals. However, these patterns are not set rules. Recent field studies report the use of small chirps paired with HFBs during courtship, a behavior not previously reported in lab studies, and therefore not previously examined in detail (Henninger, 2015; Henninger et al., 2017 preprint). Given the nature of the signals and the neural responses described in this Introduction, this system allows us to ask if the neural code employed is simply a function of the signal or whether it is dependent on context and consistently matched to the behavioral task in order to enhance either the capacity to discriminate or simply detect the stimulus.

MATERIALS AND METHODS

Animals

The weakly electric knifefish *Apteronotus leptorhynchus* (Elliss 1912) was used for all experiments. Animals were wild-caught and purchased from a tropical fish supplier (Segrest Farms, FL, USA). Fish were maintained in a home tank (61×30.5×50.8 cm) at 26–27°C, 250–300 µS according to West Virginia University IACUC guidelines (protocol 1512000009.2).

Neurophysiology

Surgical methods are based on those described in Marsat et al. (2009) and Marsat and Maler (2010). Fish of both sexes were anesthetized and respirated with a solution of Tricaine-S (tricaine methanesulfonate, Western Chemical, Inc.) in water (0.25 g l^{-1}) for the duration of the surgery. After the application of a local anesthetic (Lidocaine HCl 2%, Hospira, Inc.), skin and overlying soft tissues were removed from a small area of the skull. A portion of the exposed skull was glued to a fixed post for stability while the portion of the skull overlying the ELL was then removed. Fish were immobilized with a 0.1 ml injection of Tubocurarine chloride pentahydrate (0.2 mg ml^{-1}, TCI), switched to anesthetic-free water for respiration, and allowed to recover from surgery for approximately 20 min in the experimental tank before stimulation and recording. The experimental tank (40×45×20 cm) contained water matched to the home system. *In vivo* recordings of the lateral segment (LS) of the ELL were made via metal-filled extracellular electrodes (Frank and Becker, 1964) and amplified (A-M Systems, Model 1700), and data recorded (Axon Digidata 1500 and Axoscope software) at a 20 kHz sampling rate. Pyramidal cells of the LS were targeted and identified by location in relation to major surface blood vessels, depth from the surface of the brain, as well as neural response properties (Maler et al., 1991; Saunders and Bastian, 1984).

Stimulation during neurophysiology

All stimuli were sampled at 20 kHz and created using MATLAB (MathWorks, Inc.). Pyramidal cells respond to changes in EOD amplitude (Bastian, 1981; Saunders and Bastian, 1984), so stimulation was provided by a direct modulation of a carrier frequency matching the fish's own rather than by mimicking a second EOD. This method allows for tight control over the signal the fish receives and is commonly used in similar experiments (Bastian and Heiligenberg, 1980; Benda et al., 2005). Although this stimulation method does not replicate the phase modulation component of natural communication signals, only T-unit electroreceptors encode this stimulus feature. Very few T-unit electroreceptors are found in *A. leptorhynchus* and they do not provide direct inputs to pyramidal cells (Maler et al., 1981). P-unit receptors [those that encode amplitude modulation (AM) signals] drive pyramidal cells. These electroreceptors respond in an identical manner to AM only or AM+EOD phase stimuli (Benda et al., 2005). The responses of the pyramidal cells to these types of stimuli are not significantly different (our unpublished results: see Marsat et al., 2014)

The baseline EOD was recorded via electrodes near the head and tail of the fish. Each EOD cycle triggered a sine wave generator (Rigol DG1022A) to generate one cycle of a sine wave matched to the animal's own. This signal was then multiplied using a custom-built signal multiplier (courtesy of the Fortune Laboratory, New Jersey Institute of Technology) by the AM stimulus to create the desired modulation of the electric field around the fish. It was played through a stimulus isolator (A-M Systems, Model 2200) into the experimental tank via two 30.5 cm electrodes. The electrodes were placed on either side of the fish close to the tank walls and parallel to the fish's longitudinal axis. This arrangement produces a fairly uniform stimulation of the majority of the skin's surface. The stimulus strength was adjusted to provide ∼20% contrast (the difference between the maximum and baseline EOD amplitude relative to baseline).

Chirp stimuli consisted of a Gaussian-shaped frequency modulation of the background beat presented once per second on either a 10 Hz (low-frequency beat; LFB) or 120 Hz beat (high-frequency beat; HFB). The frequency and duration of chirps were chosen to mimic a range of natural signals (Bastian et al., 2001). Small chirps were either 10 ms long with a 60 Hz increase, or 15 ms long with a 122 Hz increase. Big chirps were either 15 ms long with a 300 Hz increase, or 45 ms long with a 900 Hz increase. Chirp frequency increase was tied to a signal amplitude decrease of 0.08% for each Hz of frequency rise, based on natural chirp properties (Zupanc and Maler, 1993). All four chirps were played on both the 10 and 120 Hz beats but responses to big chirps on the 10 Hz beat were not examined in detail. Small chirps were presented at several different phases of the beat, typically at the peak or trough of the sine wave.

The present study is not intended as an exhaustive characterization of responses to chirps as this information is already available (e.g. Marsat and Maler, 2010; Marsat et al., 2009; Metzen et al., 2016; Vonderschen and Chacron, 2011). Rather, we used a single pair of chirps for each stimulus category and chose the chirp properties of the pair to be as different as possible in both duration and frequency increase given observed natural ranges (Bastian et al., 2001). This makes the discrimination task as easy as possible for the animal while keeping the chirp properties realistic for each category.

Neural data analysis

Analysis of discrimination (shown in Figs 1–3) is based on Marsat and Maler (2010) and modifications to methods originally described by van Rossum (2001). This method accounts for both the firing rate as well as the temporal pattern of spikes to quantify how similar or dissimilar spiking patterns are. Our analysis is mathematically equivalent to previous approaches (Laubach et al., 2000; Stecker et al., 2005; Tremere and Pinaud, 2011; Vonderschen and Chacron, 2011) but instead of displaying a confusion matrix and calculating the amount of information carried by the population response about stimulus identity, we display the ROC curves and quantify an error level.

Spike trains were binarized and convolved with an α filter, $f(t)=t^{-2.45/\tau}$, with τ being the width of the function at half maximum (Machens et al., 2003). A portion of the result $R(t)$ was extracted for analysis, specifically, a window around the timing of the presented chirps (−15 to 30 ms relative to the middle of big chirps and −10 to 30 ms relative to small chirps). The distance D_{xy} between the two spike trains x and y of length L is defined as: $D_{xy} = 1/L \times \sum_{t=0}^{L} [R_z(t) - R_y(t)]^2$. Larger distances indicate more dissimilar spike trains. In addition to the response of

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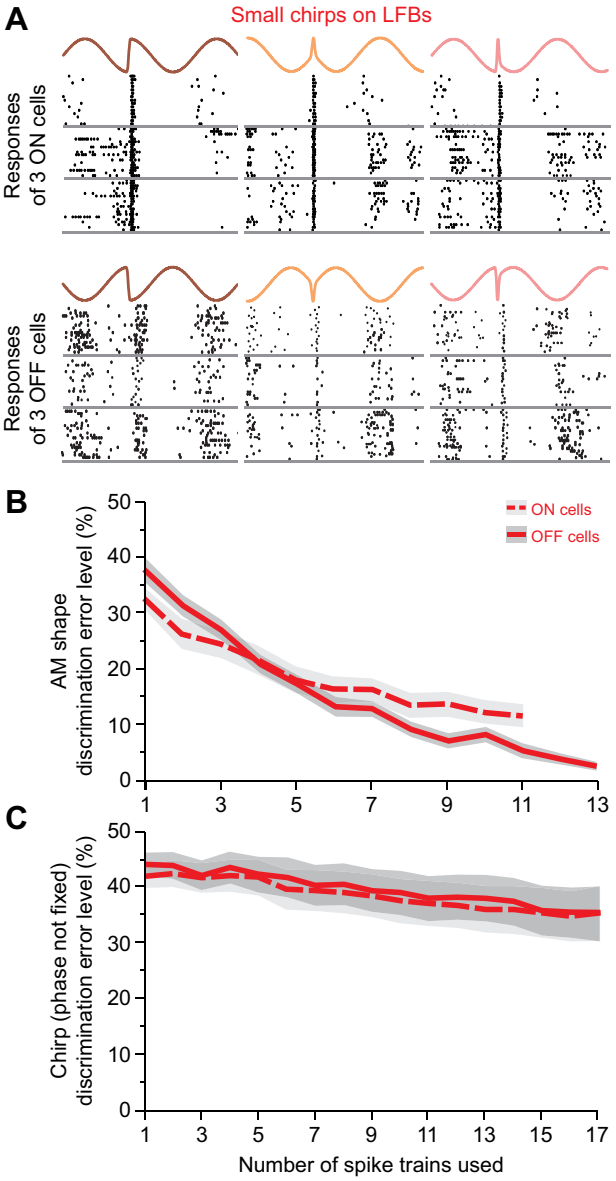

Fig. 1. Small chirps cannot be discriminated when presented on LFBs in a realistic manner. (A) Example responses of 3 ON cells (top) and 3 OFF cells (bottom) stimulated with small chirps on a 10 Hz beat. The phase at which the chirp occurs changes the shape of the signal, even when the chirp frequency and duration are the same. Note that the chirps on the left and right have the same properties but are presented at different phases while the chirp in the middle differs in both duration and frequency. (B) Discrimination analysis performed on spike train responses to chirps varying in both duration and frequency but occurring at the same phase. Shaded area indicates standard error. (C) Discrimination accuracy for chirps with varying parameters when phase is not kept fixed. This scenario reflects the most natural aspects of chirp occurrence. Since chirps are not produced at specific phases, discrimination of chirp features would have to happen despite the variability of starting phase. Error level remains close to chance (50%) even when many spike trains are recruited.

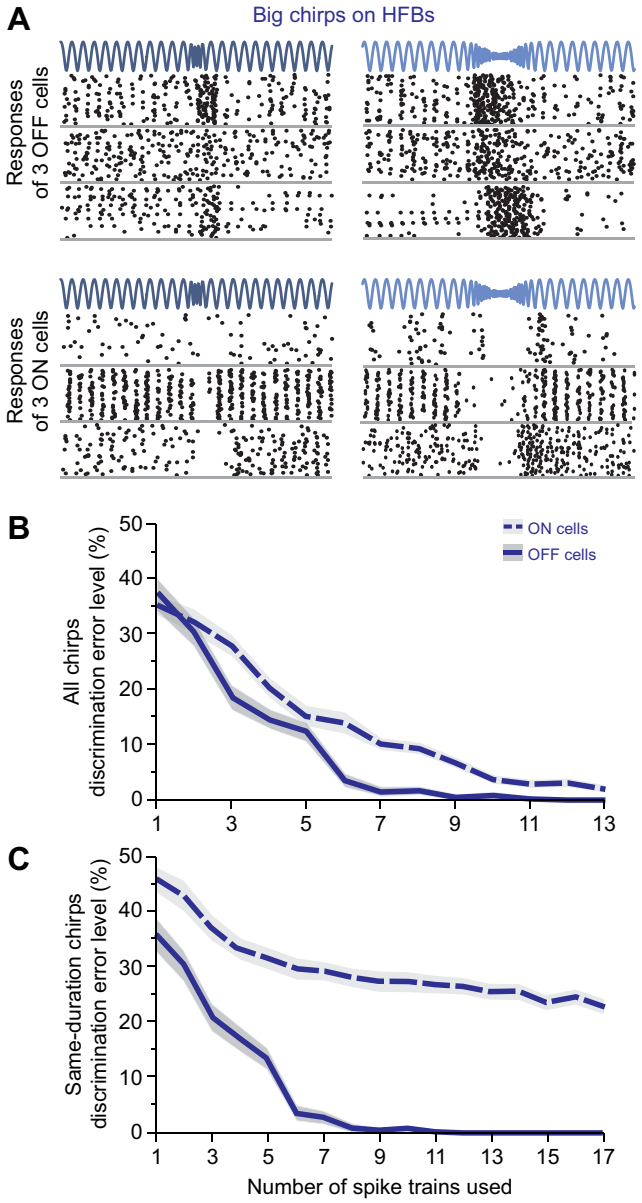

Fig. 2. Big chirps on HFBs are discriminated efficiently. (A) Example responses of 3 ON and 3 OFF cells to big chirps that vary in both frequency and duration and that occur on a 120 Hz beat. Big chirps variably increase OFF cell firing rate. ON cells are inhibited by big chirps. (B) Chirps that vary in both duration and frequency rise are discriminated by both ON and OFF cells. (C) Chirps that vary only in frequency, but not duration, can only be discriminated by the graded responses of OFF cells. Shaded area indicates standard error.

individual neurons, we looked at population responses by averaging several spike trains using the function $PR(t) = \sum_{i=t}^{n} [Ri(t)]/n$. The result $[PR(t)]$ represents a population of neurons presented with the same stimulus and mimics a neuron integrating postsynaptic potentials with similar weights (Larson et al., 2009). These population responses were created by randomly pairing multiple individual responses, simulating the response of a diverse population of cells. Up to 200 random combinations of spike trains from all recorded neurons were used for all comparisons. Responses to different chirps (X versus Y) were compared as well as multiple responses to the same chirp (X versus X). Distance (D_{XY} or D_{XX}) was calculated for all sets of combined responses, $PR_x(t)$ and $PR_y(t)$, creating an array of response distances for each comparison. The probability distributions of the values in these arrays [$P(D_{XY})$ or $P(D_{XX})$] were used for ideal observer analysis. Receiver operating characteristic curves were generated by varying the threshold distance for discrimination, T. For each threshold value, the probability of non-discrimination (P_D) is calculated as the sum of $P(D_{XY}>T)$, and the probability of false discrimination (P_F) as the

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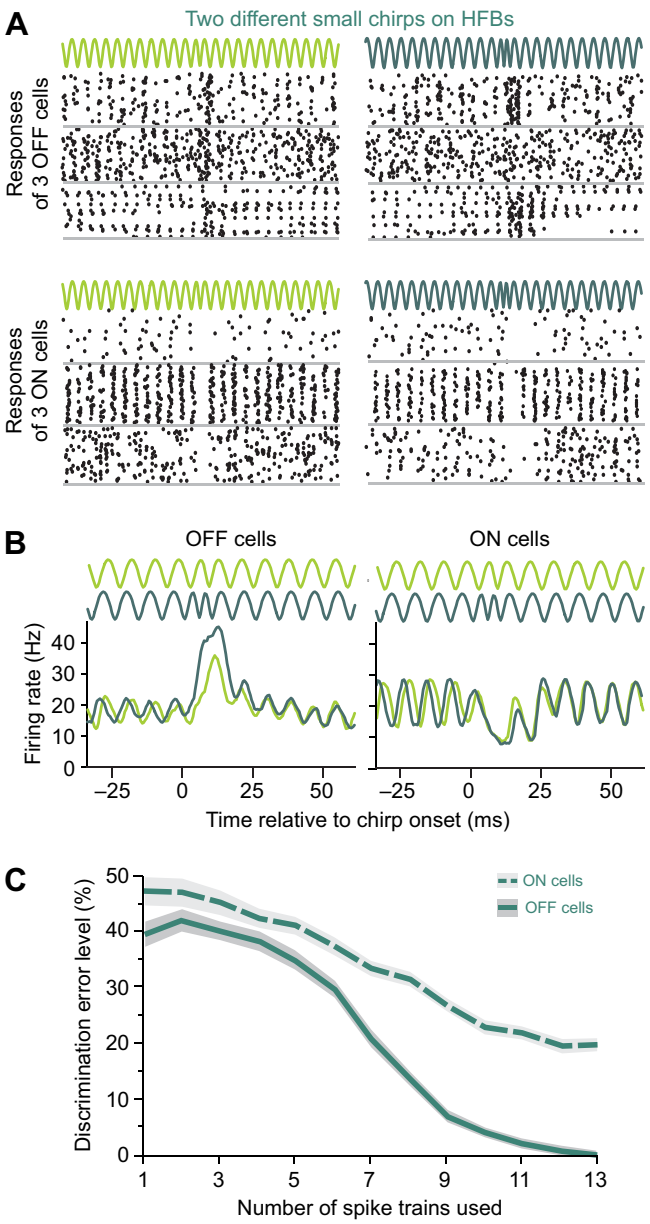

Fig. 3. Small chirps on HFBs can be discriminated and are coded by graded responses. (A) Example responses of 3 ON and 3 OFF cells to small chirps on 120 Hz beats. Similarly to big chirps, ON cells are inhibited, and OFF cells show varied increases in firing rate. (B) Average firing rate for OFF (left) and ON cells (right) during presentation of two different small chirps. There appears to be a greater difference in averaged responses for OFF cells compared with ON cells. (C) Discrimination performance based on the response of ON and OFF cells. OFF cells can discriminate between varying small chirps on HFBs with more accuracy than ON cells. Shaded area indicates standard error.

sum of $P(D_{XX}>T)$. The error level for each threshold value is $E= ½P_F+ ½(1−P_D)$. The error in discrimination reported in the figures are the minimum values of E. This measure of error rate is closely related to the Kullback–Leibler divergence quantifying how much overlap two distributions have. These measures thus quantify how different two distributions are without relying on assumptions of normality as other statistical tests often do. Jackknife resampling (leaving one neuron at a time out of the analysis) was used to calculate the standard errors displayed in Figs 1–3. Sample sizes for these figures are equal to the maximal value of the x-axis plus one.

Even though it is relatively simple, our spike metric distance analysis is based on a principle that can be implemented by a biologically realistic decoder (Larson et al., 2009). More complex decoders that could be implemented by neural circuits have been tested but failed to allow discrimination of small-chirp LFB signals (our unpublished results; see Sharpee et al., 2016).

Behavioral paradigm

The experimental tank measured 30 cm×30 cm×10 cm and contained water matched to the fish's home tank. Fish were allowed to acclimate overnight. The experimental tank was shielded from light and illuminated with an infrared light source and filmed with an infrared camera (Logitech C920, with its IR filter removed). Video was captured at 24 frames s^{-1} and a spatial resolution of 1280×720 pixels (the tank covered the width of the frame). Stimuli were played via a pair of submerged electrodes (dipole spacing=10 cm) located in one quadrant of the tank (Fig. 4A) at a strength replicating the average fish's electric field. The small size of the behavior tank ensures that no matter where the fish is positioned in the tank, the stimulus received will be fairly strong and should not affect the reception of the chirp stimulus.

Fish were played one of three chirp stimuli: big chirps on a 120 Hz beat, small chirps on a 10 Hz beat, or small chirps on 120 Hz beat. Chirp properties were as described for the neurophysiology experiments. These chirps were played at a rate of twice per second for one minute, followed by a 2 min break with no stimulation. This stimulation pattern was repeated for 90 min to habituate the fish to the chirp. After 90 min, a chirp of the same category (either small or big) but with a different frequency increase and duration was played on the same beat frequency (Fig. 4B). Behavior was assessed throughout the experiment when the stimulus was ON to quantify the habituation and possible dishabituation of the response. Recordings were acquired from 250 trials. A given fish was tested only once a day and could be tested up to three times, once with each stimulus.

Behavioral analysis

The video files were imported in MATLAB where a custom program was used to analyze the video frame by frame. The semi-automatic analysis identified the position of three points on the fish: the tip of the nose, the tip of the tail and the 2D center of mass. These points were determined automatically by the program but visual inspection of the results was required to correct occasional errors (e.g. flipping of the tail and nose). Swimming speed and position could easily be calculated given the frame time stamp and the spatial calibration. The results displayed took into account the position of the nose, but the 'center of mass' gave similar results; results using the tip of the tail were not evaluated.

For each 1 min stimulus bout, the swimming speed was calculated (Fig. 4) based on the distance moved between video frames. A probability distribution of swimming speed for each stimulation bout was then calculated. When the fish was swimming actively (relatively high speed), we noticed that the strength of the overall response was not most strongly correlated to the swimming speed, but rather that the time spent swimming actively at relatively high speed was a better indication of the response strength. To quantify swimming speed in a way that accounts for these characteristics, we calculated a relative swimming speed ratio. Using the three stimulation bouts preceding the chirp-change (i.e. habituated state) we calculated a median swim speed and used it as a threshold to define two ranges of speed: slow or fast. We defined a speed index as the ratio of the proportion of time where swimming is

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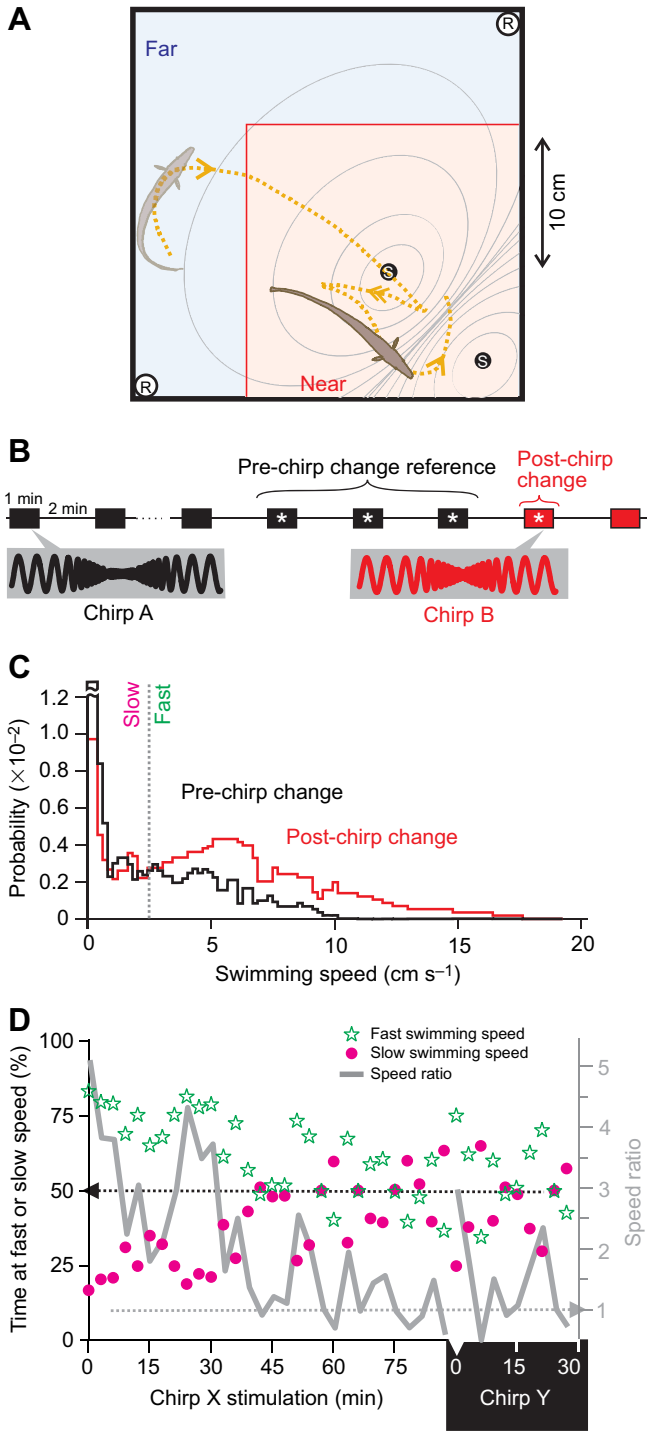

Fig. 4. Experimental design for habituation–dishabituation trials. (A) Schematic of the experimental tank. Recording electrodes (R) recorded electrical activity as the fish swam freely (example track shown in yellow). Stimulating electrodes (S) were located in one corner of the tank, creating a fish-sized field potential (isopotential field lines illustrated in gray). Two zones, far (blue) and near (red) were defined, splitting the tank on two equal areas relative to the stimulus. (B) Chirp stimuli were played 1 min on, 2 min off for 90 min (black boxes). After 90 min, a stimulus of the same chirp category but with different properties was played (red boxes). Asterisks indicate stimulation bouts used to define pre-chirp change and post-chirp change responses. (C) Example of swimming speed distribution during the habituated (black) phase of the stimulation and the first stimulus presentation after changing chirp properties (red). The median of the swimming speed in the three stimulation bouts prior to chirp-change (dashed line) is used as a threshold between slow and fast swim speed. (D) Speed ratio is calculated by first defining fast and slow swimming speed based on the threshold defined in C. The proportion of slow swimming (circles) and fast swimming (stars) is determined for each stimulation bout. The speed ratio (fast/slow) is then calculated (gray line; see *y*-axis on the left). Responses where 50% of the swim speeds are slow and 50% are high (points on the black dotted line) lead to speed ratios of one (gray dotted line). The data presented here are noisy since they come from a single trial (the same as that used for C). Nevertheless, the trend is visible: the ratio is high in the first 30 min and drops to 1 just prior to the change in chirp. The first stimulation bout post-chirp change results in a fairly high speed ratio of 3. This procedure normalizes the speed measure for each fish and focuses on the time spend in active (fast) versus quiescent (slow) motion rather than absolute speed averages.

fast versus slow. Using the speed threshold determined from the trials preceding the chirp change allowed us to normalize this speed index to 1 for the habituated state. If the fish spends more time swimming at fast speeds, the speed index will be above 1 (e.g. index of 3 if the fish swims fast 75% of the time vs 25% at slow speed). Speed indices are not normally distributed, thus data were transformed with an exponential function to change the distribution into a normal one for statistical testing with a paired *t*-test in Fig. 5C.

Quantifying the distance of the fish to the stimulus dipole using 'mean distance' would likely give unreliable results given that the length of the fish and the spread of the dipole are large relative to the size of the tank. Instead, the position of the fish was categorized in two zones: near or far. A square area of 21 cm×21 cm centered on the corner containing the dipole defined the near region, which was of similar area as the remainder of the tank, the far zone. The fish was considered located in the zone containing the majority of the pixels representing the fish.

RESULTS

In this study, three types of communication signals were used: LFBs (10 Hz) paired with small chirps (typical of agonistic encounters), HFBs (120 Hz) with big chirps and HFBs with small chirps (both more typical of courtship). For each type, the stimulus was presented with several chirp variants, differing in duration and in frequency rise within a range typical of *A. leptorhynchus* signals. For each stimulus set, our analyses were based on the responses of 15–20 cells (either ON cells or OFF cells) recorded from the LS. Superficial, intermediate or deep cells were not targeted specifically, but baseline firing rates of 20.4±9.6 Hz for ON cells and 15.2±7.5 Hz (mean±s.d.) for OFF cells indicated that most recorded neurons were from superficial or intermediate layers (Bastian and Courtright, 1991). Using an analysis based on spike metric distances between neural responses (see Materials and Methods) we quantified the discrimination errors that an ideal decoder would make based on the information contained in these population responses. Efficient encoding should achieve low discrimination error rates based on the response of the fewest neurons possible.

Encoding of signals mediating agonistic encounters does not efficiently represent chirp properties

Small chirp stimuli cause abrupt phase-shifts in the background beat cycle (Fig. 1A). The spatial geometry of electric field and electroreceptors is such that a stimulus that increases electrical amplitude on one side of the body causes a decrease in amplitude on the other side, eliciting a response from ipsilateral ON cells and OFF cells, respectively. As we have shown previously (Marsat et al.,

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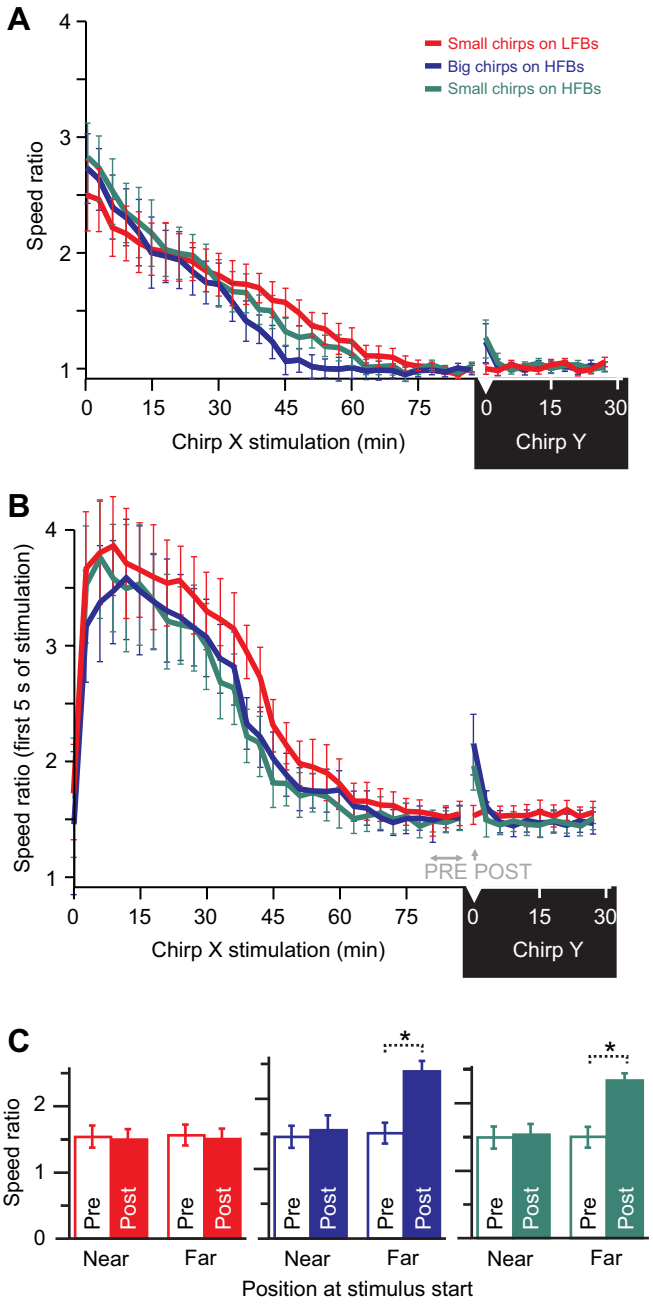

Fig. 5. Both small chirps and big chirps on HFBs cause dishabituation. (A) Average speed ratio as a function of stimulation bout. LFB stimuli show no dishabituation, HFB stimuli show small, but non-significant effects. (B) Average speed ratio during the first 5 s of each stimulation bout. Speed increases for novel chirps on HFBs indicate dishabituation. (C) Fish farther from the stimulating electrodes at start of the novel chirp increase speed only for chirps on HFBs. See key in A; dotted brackets with asterisks indicate significant differences (average±s.e.; paired *t*-test, $P<0.01$). For each stimulus category, 80 to 85 trials were conducted; in each category 43–56% had fish classified as far from the dipole just prior to the start of the novel stimulus.

2009), superficial ON cells of the lateral segment of the ELL respond with a more salient response than other cells in the ELL: they produce a high-frequency stereotyped burst of spikes after the chirps that serves as a particularly effective chirp-detection mechanism. Both the bursting and non-bursting responses contained some information about the AM shape of the chirp stimulus. However, these response types still led to error even when pooling the responses of 13 cells, with ON cells producing much less discriminable responses than OFF cells (Fig. 1B). The analysis in Fig. 1B used the same procedure as Vonderschen and Chacron (2011) and the results are qualitatively similar. However, information about AM shape of a chirp did not allow an observer to discriminate differences in the parameters such as differences in duration or frequency rise (Fig. 1C). For these stimuli, a chirp with specific duration and frequency occurring at a given phase will cause a different AM shape compared with the same chirp with identical frequency and duration properties occurring at another phase (compare the first and last stimuli in Fig. 1A). Consequently, two chirps that differ in parameters the animal can control (duration, frequency) could elicit responses that are more similar to each other than to the response of identical chirps occurring at different phases (which the animal does not control) (Aumentado-Armstrong et al., 2015). A decoder cannot rely on the spiking pattern to estimate variation in these chirp signals since the relevant parameters are obscured by the phase on which the chirp occurs (Walz et al., 2013). Our results argue that the signal's characteristics hinder discrimination and this signal is thus encoded with a synchronized bursting code that is efficient for detection (Marsat et al., 2009) but less so for discrimination (Fig. 1B). The characterization of the responses to these signals is the topic of a previous publication (Marsat et al., 2009), so we will not explore it in depth here. Not all neurons burst in response to these chirps, and the coding scheme we describe here is not crucially dependent on the neurons bursting, but rather on them having a relatively homogeneous response across chirps. Other studies indicate that these signals do indeed lead to correlated activity across the population, consistent with our findings (Metzen and Chacron, 2017).

Chirp properties are accurately encoded in high-frequency beat contexts

Big and small chirps occurring on HFBs span several cycles of the beat and thus the overall AM shape of the signals is virtually unaffected by the phase at which the chirp started (Walz et al., 2014). Big chirps cause a transient increase in beat frequency that is also accompanied by a decrease in the beat amplitude directly proportional to the frequency increase (Zupanc and Maler, 1993). These chirps caused a graded increase in firing rate in OFF cells and a cessation of firing in ON cells (Fig. 2A). The increase in OFF cell firing ranged from only a few Hz in some cells or a few hundred Hz in others (Marsat and Maler, 2010). For chirps that differ in duration and frequency, ON and OFF cells both allowed accurate discrimination based on the responses of 12 cells (Fig. 2B). The duration of the break in firing in ON cells was proportional to the duration of the chirps, thus carrying information about chirp duration, but not frequency increase. Note that in some ON cells, particularly superficial cells, the pause in firing was followed by an increase in firing rate that seems correlated, within a cell, to the duration of the pause. The role of this delayed aspect of the response is unclear and has not been explored further. When presented with two chirps that do not differ in duration but only in frequency, the pause in ON cell firing cannot allow accurate discrimination. OFF cells responded in a graded manner, increasing firing in relation to both chirp duration and frequency increase, allowing for efficient discrimination even when chirp duration is identical (Fig. 2C). These data show that big chirps on HFBs are encoded with spiking patterns that allow the identification and discrimination of chirp characteristics.

Even though small chirps and big chirps are categorically different signals that often mediate different behaviors (Hagedorn

and Heiligenberg, 1985; Hupé and Lewis, 2008), their behavioral impact (Dunlap and Larkins-Ford, 2003; Triefenbach and Zakon, 2008, 2003) and the way they are encoded in the electroreceptors (Benda et al., 2006) depends on the beat frequency. Specifically, in the electroreceptors, small chirps on LFBs cause an increase in synchrony among receptors, whereas both small chirps and big chirps on HFBs cause a decrease in synchrony (Walz et al., 2014). We see a similar separation of the responses in the ELL: the responses to small chirps on HFBs were more similar to big-chirp responses rather than to responses to small chirps on LFBs. OFF cells responded with an increase in firing and ON cells with a pause in firing (Fig. 3A). The small chirps shown in Fig. 3 caused an increase in firing of 20 Hz on average in OFF cells, which corresponds to a doubling of baseline frequency. This increase appeared slightly stronger and longer in the larger of the small chirps. We calculated the instantaneous firing rate of population responses that included 12 neurons and averaged them across possible combinations and repeats (Fig. 3B) to estimate the variability in the time course of the population response's firing rate. As described in the past for the response of OFF cells to big chirps (Marsat and Maler, 2010), this population response was relatively invariant from trial to trial; therefore, the difference in response shape for the two small chirps was larger than the typical variability in the response to a given chirp. Quantification of this observation in Fig. 3C shows that discrimination error level based on spiking pattern differences reached very low values for OFF cell population responses of 12 neurons or more. ON cell responses have a difference in the time-course of the population instantaneous firing rate but it was small relative to the variability in the pattern of responses to the same stimulus and thus the discrimination remained inaccurate. It is possible that larger populations of responses (much more than 13 cells) could lead to error-less discrimination, presumably by partially averaging out the variability in the population response. Therefore, we conclude that both ON cells and OFF cells can support the discrimination of small chirps on HFBs but that OFF cells do so more efficiently.

Correlating behavior with coding strategy

Our neurophysiological data argue for a match between a signal with a structure that hinders discrimination (small chirps on LFBs) and a neural code that is not efficient at supporting discrimination (Fig. 1B) but rather geared towards sensitive detection of the stimulus (synchronized bursting). In contrast, signals with structures well suited to being discriminated are encoded with graded heterogeneous responses that efficiently carry information about chirp characteristics, thus allowing discrimination of chirp variations. Despite this compelling evidence that neural codes and signal structures are matched to support different tasks, discriminating versus simply detecting the signals, it is unclear whether it actually mediates different behavioral responses and perceptual tasks. The neurophysiological results predict that some stimuli can be discriminated, but not others; therefore, we tested the fish's ability to discriminate. We specifically hypothesized that the fish will not discriminate between different small chirps on LFBs but that small chirps on HFBs will be discriminated, as will big chirps on HFBs.

To test this prediction, we used a paradigm that has been used successfully in a wide variety of animals and modalities to test perceptual discrimination abilities: a habituation–dishabituation assay (Carlson et al., 2011; Cheney and Seyfarth, 1988; Miller-Sims and Bottjer, 2012; Penn and Potts, 1998; Wyttenbach et al., 1996; Zuberbühler et al., 1999). The test relies on the fact that animals respond most strongly to novel stimuli and habituate to a stimulus that is presented, unchanged, repeatedly. In the steady, habituated state, the animal responds relatively weakly or not at all to the stimulus. When presented with a novel stimulus, the animal displays a resurgence of response that reflects the fact that the animal perceives the stimulus as novel. This dishabituation response – or lack thereof – demonstrates that the animal discriminated – or not – between the first and second stimulus. One of the strengths of this assay is that it takes advantage of the animal's innate response to a stimulus. The test therefore reveals how perceptual abilities are used to guide innate behaviors. In this case, sensory information about a stimulus' novelty is used to drive an increase in behavioral response. We took advantage of the fact that most *A. leptorhynchus* fish placed in a confined space (here, an aquarium of 30 cm×30 cm×10 cm) will react to a conspecific signal by increasing swimming movement and speed, swimming around the source of the stimulus as if 'investigating' and sometimes chirping, biting or lunging in that direction (Fig. 4A). Our repeated stimulation protocol (Fig. 4B, see Materials and Methods for details) elicited responses that habituated and reached a steady state within 60–70 min. Therefore, after 90 min of stimulation with a given chirp, the stimulus was switched to a stimulus with the same beat frequency (HFBs versus LFBs) and the same chirp type (small versus big) but different chirp parameters (frequency rise or duration). We used the same stimuli as in the neurophysiological experiments.

Swimming speed changes reveal perceptual discrimination of chirps on high-frequency beats

Various aspects of the behavioral response were quantified and several showed some habituation–dishabituation effect (biting, lunges, chirping; data not shown). Counting lunges or chirps clearly showed habituation, but only revealed dishabituation in a small subset of individuals. If the dishabituation response was not strong enough to cross the threshold where it would produce one of these highly aggressive behaviors, the measure would not reveal the phenomenon. We found swimming speed and changing distance from the stimulus source were more sensitive measures of dishabituation.

The distribution of swimming speeds during a given stimulation bout typically had a bimodal form with a peak at slower swimming speed indicative of a passive state and the faster swimming speed occurring during active swimming (Fig. 4C). We took the ratio of time spent in these two states (normalized for each fish) to quantify the strength of the behavioral response (Fig. 4D, see Materials and Methods for details). The ratio was higher than 1 at the beginning of the assay when the fish reacted most strongly (i.e. swam faster) to the stimulus and also if the fish exhibited dishabituation to the novel stimulus.

Swimming speed decreased markedly in the first hour of stimulation (Fig. 5A). There was no significant difference in average swimming speeds across stimulus types at the beginning of the stimulation protocol (ANOVA for time 0 of chirp X stimulation: P=0.3) and, by design, reach the same speed ratio of 1 by the end of the habituation period. Although the change in speed across the habituation period was very similar across the three stimuli, the fish might have habituated slightly slower to LFBs. This observation is supported by the fact that a few data points around 45 min are significantly higher for the LFB stimulus compared with big chirps on HFBs for Fig. 5A or small chirps on HFBs in Fig. 5B (MANOVA followed by Tukey HSD with significance set at P<0.05).

The first stimulus bout with a new chirp led to a small increase in speed ratio for both small and big chirps on HFBs but not for small

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chirps on LFBs. (MANOVA followed by Tukey HSD showed $0.15<P<0.32$ between the HFB stimuli at time 0 of chirp Y and the last three stimulus presentations of chirp X. For LFB stimuli, the same comparison gave $0.36<P<0.42$.) The small increase for HFBs was not significant because two factors affect the magnitude of this dishabituation effect. (1) The dishabituation response is marked in the first few seconds of stimulation but disappears quickly. Since each data point in Fig. 5A is an average across the whole 1 min of stimulation, the short dishabituation effect did not influence the values very much. (2) Dishabituation was observed more clearly in some fish than in others as a function of the position of the fish when the new stimulus starts (see next paragraph and Fig. 5C). To account for the fact that behavioral responses were the strongest at the beginning of each 1 min stimulation bout and that the dishabituation effect was short-lived, we quantified speed ratios in the first 5 s of each bout (Fig. 5B). These behavioral responses show a similar habituation trend that plateaued after 60 min. The dishabituation when the new stimulus was played was obvious and significant for chirps on HFBs but not for small chirps on LFBs. (MANOVA followed by Tukey HSD showed $0.02<P<0.04$ between the HFB stimuli at time 0 of chirp Y and the last three stimulus presentations of chirp X. For LFB stimuli, the same comparisons give $0.27<P<0.45$.)

Reaction of the fish to a novel stimulus depends on its distance to the stimulus source

When trying to identify the factors that could influence the variability in the observed behavior, we noticed that some fish did not show a recovery of active swimming when the new stimulus was played. In every case, the fish was close to the stimulation electrode just before the start of the new stimulation. In contrast, fish that were further from the electrode reliably started to move actively towards the stimulation electrode when a new chirp on HFBs was delivered. We quantified this by separating the trials based on the position of the fish in the 1 s prior to the start of the new stimulus. Trials where the fish had over 50% of its body length in the 'far' zone (Fig. 4A) were categorized as such whereas in the other trials the fish were defined as being 'near'. We contrasted the speed ratio in the three stimulation bouts pre-stimulus change (only the first 5 s were taken into account as in Fig. 5B) to the swimming speed in the first seconds of post-chirp change stimulation. Our data confirm that dishabituation was observable only if the fish was not in close proximity to the stimulation electrode (Fig. 5C, paired *t*-test, $P<0.01$ for the HFB stimuli with the fish classified as 'far' and $P>0.1$ for all others). We speculate that fish that were located near the electrodes when the new stimulus was introduced could determine there were no other changes associated with the stimulus (e.g. another fish getting closer) and thus it did not need to get closer and investigate. Fish approached the novel stimulus, thus showing discrimination of chirps only on HFBs.

Position in the tank could also reveal changes in behavioral responsiveness of the fish if the fish remained near the stimulus source when actively engaged by the stimulus and less so when the behavioral response habituated. We categorized the position of the fish based on zones (see Fig. 4A and Materials and Methods), although we repeated our analysis with other ways of quantifying distance (e.g. head to middle-of-dipole distance) with qualitatively similar results. The overall fish position did not change as the fish habituated to the stimulus (Fig. 6A). When swimming actively, the fish often directed its movement towards the electrodes but also swam to and fro and often circled the stimulation zone, which resulted in a relatively spread distribution of position overlapping

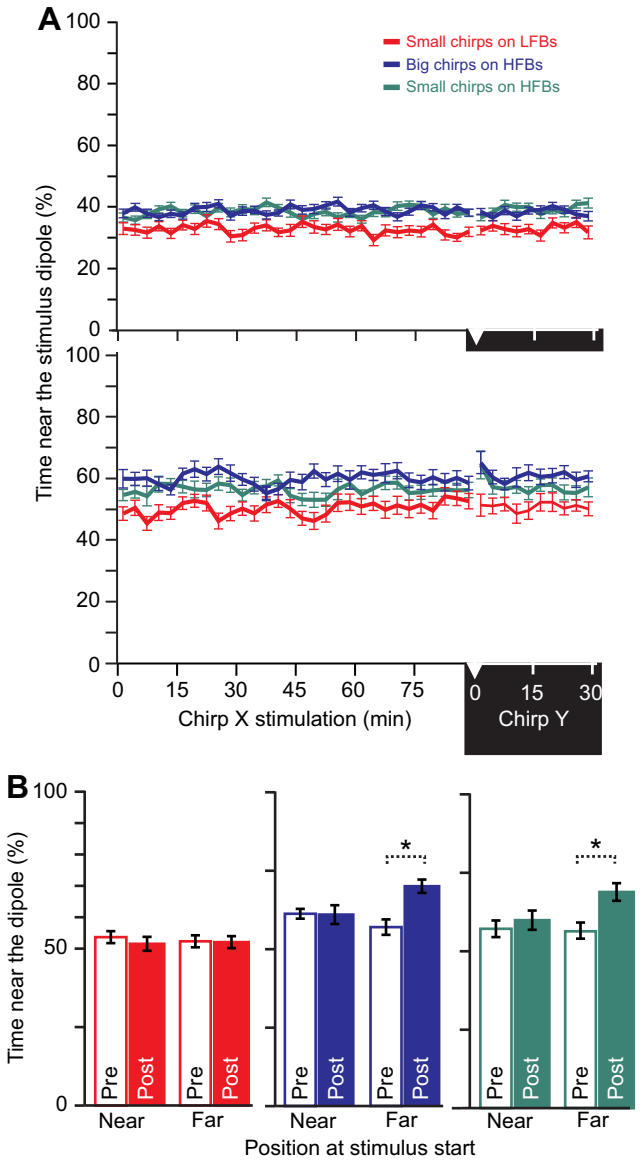

Fig. 6. Fish change location in the tank with dishabituation. (A) Time spent in the area near the stimulation dipole for each bout in the sequence averaged across all fish. Fish typically spent 30–60% of the time near the stimulus dipole but position did not change with repeated stimulation. This lack of habituation across stimulation bouts is observed whether using the entire recording (top panel) or the first 5 s (bottom panel). (B) Position of the fish during stimulation for stimuli preceding novel chirp (white bars) or following novel chirp (filled bars) for fish far or near the stimulation source just prior to stimulus onset. See key in A. Using the first 5 s of stimulations, data show that fish farther from stimulating electrodes at the start of the novel chirp moved closer for chirps on HFBs. Dotted brackets with asterisks indicate significant differences in the time spent near the stimulus source (average±s.e.; paired *t*-test, $P<0.01$).

both near and far zones. When responding less strongly (e.g. in habituated state) the fish often remained still on one side of the tank. Each fish had its preference as to which side it chose (near or far from the electrodes), leading to a broad distribution of positions. Nevertheless, by selecting the first five seconds of each stimulus and categorizing the trials based on position just prior to the new stimulus (as in Fig. 5C) we saw a change in the position of the fish in response to changes in HFB stimuli (Fig. 6B). This is consistent with the scenario that led to the results in Fig. 5C: in the first few seconds of a new HFB stimulus, if the fish was far from the electrode

it swam towards the electrode and passed over it several times presumably to investigate the source of the new stimulus.

DISCUSSION

Our data demonstrate a clear link between the perceptual responses to a communication signal and the neural response patterns encoding that signal. Our electrophysiological recordings show that two discrete patterns of firing encode chirps: one code with high information content (heterogeneous and graded changes in firing) about chirp details and one with low information content about chirp properties (synchronous bursting). The behavioral response of the fish shows that these two codes mediate different perceptual tasks. The fish tested were able to perceive and react to slight differences in chirps that are encoded via graded heterogeneous firing rates. Chirp stimuli that elicited stereotyped bursts, however, did not result in discrimination behavior. This change in coding strategy is mediated by the beat frequency on which the chirp is presented. This is not simply a consequence of the chirp characteristics itself but also depends on the background beat which sets the context: an individual with similar EOD frequency (i.e. most likely an individual of similar sex and maturity) or not.

Neural coding is matched to signal structure

Small chirps occurring on LFBs cause large shifts in the background beat, but vary dramatically in the shape of the electrical image depending on the phase of the beat on which they occur. This phase variance masks properties of small chirps such as duration and frequency rise. Emitting fish do not actively control which phase of the beat they chirp on (Aumentado-Armstrong et al., 2015; Walz et al., 2013). Likewise, a given small chirp presented at different phases is encoded in an invariant manner in the midbrain and elicits invariant behavioral responses in the receiving fish (Metzen et al., 2016). The lack of phase control in chirp behavior, and invariance of response in the physiology demonstrates that phase is most likely not relevant to either the emitting or receiving fish. It does, however, actively hinder the ability to discriminate chirp properties.

The transient disruptions caused by a small chirp on the slow ongoing background frequency cause a brief synchronization in the firing or quiescence of the electroreceptor afferents (Benda et al., 2005, 2006). Likewise, pyramidal cells respond with stereotyped (Marsat et al., 2009) and highly correlated responses across the population (Metzen et al., 2016). The brief durations of small chirps in conjunction with the long cycles of LFBs drastically impairs discrimination of chirp parameters such as duration and frequency. Our data confirm the results of Marsat and Maler (2010) demonstrating that responses to small chirps on LFBs cannot be discriminated from one another by a biologically realistic decoding mechanism.

Since we performed single-cell recording rather than multi-unit recordings, we cannot take in account the effect of noise correlation on population coding. For spatially diffuse signals such as communication signals, the amount of noise correlation has been shown to be relatively small (Simmonds and Chacron, 2015) and limited to neurons with overlapping receptive fields (Chacron and Bastian, 2008). We therefore expect the influence of noise correlations to be small. Furthermore, noise correlations would most likely deteriorate coding further for a population of pyramidal cells of a single – ON or OFF – type since their stimulus-driven response will be correlated (for a thorough discussion of noise correlations see Averbeck et al., 2006). Most importantly, no effect of noise correlations can circumvent the main factor that prevents these signals from being discriminated: the fact that the signal itself impedes discrimination, as explained above.

At higher beat frequencies both big and small chirps span more than one beat cycle, reducing the effect of phase on the electrical image the fish receives. This change in the signal structure allows the system to encode details about chirp duration and frequency. At these beat frequencies, electroreceptor afferents phase lock more synchronously to the beat than to the chirps; both small and big chirps disrupt that synchrony (Benda et al., 2006; Walz et al., 2014). Desynchronization in afferent firing gives rise to the observed ON cell inhibition and variable increase in OFF cell firing that occurs in response to both chirp types on HFBs. The variability of the response to chirps on HFBs was observed first for big chirps (Marsat and Maler, 2010) and confirmed for small chirps (Metzen and Chacron, 2017). This graded OFF cell response provides sufficient information for a decoder to accurately discriminate between big chirps. Here, we demonstrate that this coding strategy is not specific to big chirps, but is also observed for small chirps. The change in chirp structure and, as a result, the change in coding, is a product of the social context (beat frequency) rather than due to the properties of the chirp itself.

It should also be noted that, to date, all studies of chirp responses in the ELL have been undertaken using stationary stimuli. It is very possible that including the effects of movement may make the tasks of detection and discrimination more difficult since it would modulate the spatial and spectral characteristics of the stimulus (Fotowat et al., 2013; Kelly et al., 2008). Furthermore, it is known that movement can affect pyramidal cell responses (e.g. Clarke et al., 2014). Further studies using spatially realistic and dynamic stimuli might thus provide additional insight.

Perceptual ability corresponds to coding strategy

What could be the advantage of using two different coding strategies for the different contexts? Our results argue for the fact that the type of neural codes used in different situations should be matched to the perceptual task being performed. In diverse sensory systems including vision, audition and touch, there are demonstrable links between the stimulus-encoding strategy and the animal's sensory acuity (Adibi and Arabzadeh, 2011; Arabzadeh et al., 2003; Bendor and Wang, 2007; von Heimendahl et al., 2007). Our results systemically correlate two different neural codes with specific behavioral tasks: the ability to discriminate versus simply detecting the stimulus. Since our behavioral test measures motor output and not perception directly, we cannot exclude the possibility that fish perceived a difference in small chirps on LFBs but did not react. However, it does not affect the strength of our conclusion. The fact that the behavioral response is determined by the presence or absence of the chirp – rather than its detailed characteristics – demonstrates that the behavior is guided by chirp detection. Whether the information to discriminate is present at one point in the nervous system is irrelevant, as this information does not influence the behavior we examined. Our results suggest that different neural codes might be used in order to perform each of the two different behavioral tasks more efficiently. The results thus lead to the prediction that, in this system, there is a tradeoff between sensitive detection and accurate discrimination and coding efficiency is maintained by changing coding scheme.

Specialization of coding for separate tasks

In *A. leptorhynchus*, beat frequency establishes the social context of conspecific interaction and may function as a filter, priming the ELL for efficient, task-dependent signal processing. Different sub-populations of cells best encode the signals to be detected versus the signals to be discriminated (ON cells versus OFF cells,

respectively; Marsat and Maler, 2010; Marsat et al., 2009). However, these studies and our current results also demonstrate that the responses of both subpopulations allow detection and discrimination. Therefore, the difference in processing is not mainly a difference in the subpopulation that carries out the task, but rather a difference in response pattern and stimulus shape. In other words, the neural coding strategy changes as a function of the stimulus. Ollerenshaw et al. (2014) demonstrated in the rodent vibrissae system that adaptation changes the neural code from one primed for detection to one better able to discriminate – a change mirrored in behavioral performance. In the present case, changes in coding are not implemented by adaptation but are a consequence of the fixed properties of the network, such as feedforward frequency tuning (Walz et al., 2014) and feedback (Marsat et al., 2012). As indicated by our results, and studies of coding strategies in diverse sensory systems (e.g. visual: Lesica, Nicholas, Stanley, 2004; Sherman, 2001; insect auditory: Marsat and Pollack, 2004; Sabourin and Pollack, 2010), the use of different neural coding strategies for detection and discrimination tasks might be a widespread phenomenon that allows efficient coding in a constantly changing environment.

Burst firing is a particularly robust method of encoding sensory information (Krahe and Gabbiani, 2004). Bursting is not an essential requirement of this coding scheme, which is characterized by highly correlated activity across the population and invariant responses across stimuli. Responses to small chirps of LFBs possess both of these characteristics (Marsat et al., 2009; Metzen and Chacron, 2017; Metzen et al., 2016). However, the bursting dynamic increases the gain for certain stimuli (Marsat and Maler, 2012; Mehaffey et al., 2005) and thus increases the saliency of the response. A feature detection coding scheme is especially useful when encoding transient, but important, communication signals (Marsat et al., 2009) or small prey items (Oswald et al., 2004). In this light, the stereotyped burst response produced by small chirps on LFBs may reflect their ethological significance to the animal. On LFBs, indicative of same sex interactions between closely sized animals, small chirps are most commonly produced during agonistic encounters (Hupé and Lewis, 2008). Behavioral studies indicate that chirp timing is a key determinant of the interaction they mediate (Hupé, 2012). Presumably, the chirp emission pattern rather than the detailed structure of each chirp carries the information to guide behavioral responses. Detailed discrimination of these chirps may be sacrificed for reliability in detection.

The rationale for needing an efficient detection code specifically for small chirps on LFBs has not been experimentally determined yet. In the wild, small chirps are used in various contexts (Henninger, 2015; Henninger et al., 2017). They are often produced at close range (Zupanc et al., 2006), but can be exchanged between individuals as far as 30 cm away (Henninger, 2015; Henninger et al., 2017) or more (see fig. 3 in Zupanc et al., 2006). At distances of 20–30 cm, the beat contrast (i.e. effective intensity of the stimulus) can be as low as 1% (Fotowat et al., 2013). Other signals and sources of noise (e.g. another nearby fish) can also add to the sensory stream. A chirp in this weak signal, possibly embedded in noise is likely to activate the sensory system only weakly and thus a sensitive detection mechanism might be beneficial.

Burst structure is stereotyped, and in large part dictated by the burst mechanism. While some stimulus features may be extracted from bursts (e.g. Marsat and Pollack, 2010; Martinez-Conde et al., 2002; Oswald et al., 2007), they are limited in the amount of information they can encode in their interspike interval as a result of their stereotyped structure. Discrimination tasks therefore benefit from an alternative form of coding. Highly variable population responses with graded heterogeneous responses are well suited for that purpose since they accomplish signal whitening (Marsat and Maler, 2010) and thus maximize channel capacity (Doi and Lewicki, 2014; Simoncelli and Olshausen, 2001). The heterogeneity of the population has been highlighted in several publications (Bastian and Nguyenkim, 2001; Ly and Marsat, 2017; Metzen and Chacron, 2015; Sproule and Chacron, 2017). The heterogeneous responses of the population may sacrifice the reliability of detection through burst for the detailed coding of chirp features. Supporting the idea that chirp detectability decreases when coding switches from a feature detection code to a graded one, Metzen and Chacron (2017) showed that detectability – or at the very least response to – small chirps decreases when the background beat is changed from low to high frequency. It is currently unknown whether chirp parameters influence behaviors such as courtship. However, given the range of parameters in chirps produced by these fish, it is not unrealistic to hypothesize that these variations carry behaviorally relevant information. Therefore, using a neural code that is efficient for discrimination could be advantageous in contexts where chirp structure can carry information

In conclusion, our data show that the perceptual ability of an animal can be linked to the use of specific coding strategies. The ability to discriminate between chirps corresponds with a graded, heterogeneous neural response that is high in information about chirp structure, while a bursting code consisting of highly stereotyped responses is used for coding signals that are not behaviorally discriminated. These two coding strategies appear frequently across many sensory systems, implying that the specialization of these two neural codes for discrimination versus detection tasks is a common phenomenon in neural systems.

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Author contributions
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